

# Herbivory in Juvenile *Ilyanassa obsoleta* (Neogastropoda)

by

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*Abstract.* The mud snail *Ilyanassa obsoleta* (Say, 1822) is unique among the typically carnivorous neogastropods in possessing a crystalline style used to digest plant material. While adults are thought to be obligate omnivores, results of three experiments indicate that juvenile *I. obsoleta* (4–6 mm shell height) are herbivores. Juveniles gained body weight and added shell material when fed monocultures of benthic diatoms (*Acanthes brevipes* and *Nitzschia* sp.). Juveniles of both *I. obsoleta* and the herbivorous mesogastropod *Littorina littorea* (Linnaeus) grew on diets of sand microflora and a filamentous green alga (*Pilinia lunatiae*). Furthermore, interspecific effects of density on growth on a sand-microfloral diet were similar to intraspecific effects, indicating that juveniles of the two species similarly exploited the same food items. Because high assimilation efficiency on a plant diet requires style presence, the similarity between the two species' growth patterns suggests that young *I. obsoleta* do not dissolve their styles as adults do. Herbivory may have permitted young *I. obsoleta*, able to compete successfully with herbivorous mesogastropods, to invade upper intertidal marsh habitats and obtain refuge from crustacean predators.

## INTRODUCTION

*Ilyanassa obsoleta* (Say, 1822) is an abundant and widely distributed mud snail on intertidal flats along the east coast of North America. The success of this species is often attributed to its unusually diverse diet (DIMON, 1905; SCHELTEMA, 1964; CRISP, 1969; CURTIS, 1980; CURTIS & HURD, 1979, 1981a). The species is unique among the typically carnivorous neogastropods in possessing a crystalline style (NOGUCHI, 1921; JENNER, 1956; CURTIS & HURD, 1979). The occurrence of this style is apparently unique among the gastropods in general in that it undergoes a cyclic formation and dissolution (ROBERTSON, 1979; CURTIS, 1980; CURTIS & HURD, 1981a). The style contains amylase used to digest plant material (YONGE, 1930; BROWN, 1969), and during its absence the gut contains proteases. A digestive rhythm allows the organism to utilize both plant and animal tissue.

Although it is well known that *Ilyanassa obsoleta* feeds on benthic algae, CURTIS & HURD (1979) found that one-year old individuals (10.8–14.8 mm shell height) grew only when fed a mixed diet of both meat (shrimp) and vegetable (spinach). They postulated that the cycling of the crystalline style was necessary for the dietary requirements of the species. The inclusion of carrion in the snail's diet is also well known but it is typically a scarce and unreliable

resource. This observation led JENNER (1956) to speculate that the snail may obtain most of its nutrition from microorganisms in the sediment. Aptly described as a "biological vacuum cleaner" (CURTIS & HURD, 1981a), the snail consequently needs to swallow large amounts of sediment in order to obtain sufficient quantities of tiny microbes to sustain obligate omnivory.

There are size constraints to bulk deposit feeding, however. Recently settled *Ilyanassa obsoleta* (<7 mm) can apparently swallow particles of mud (<63  $\mu\text{m}$ ) but not coarser sand grains (LOPEZ, 1980). Like other tiny mud snails, young *I. obsoleta* are epistratic grazers, *i.e.*, they scrape microbial bacteria and algae attached to surfaces of sand grains (LOPEZ, 1980). Epistratic grazing is incompatible with an omnivorous diet requiring the organism to process bulk quantities of sediment.

A hypothesis not previously tested is that juvenile *Ilyanassa obsoleta* may not require animal food for growth, *i.e.*, they are herbivores. Using labeled sediment, LOPEZ (1980) found that juveniles digested microbial films of algae and bacteria, but stated that most of the label was associated with the bacteria. The present study examines growth of juveniles provided monocultures of benthic diatoms as food. The ability to grow on plant diets does not imply that the snail is normally a strict herbivore in nature,

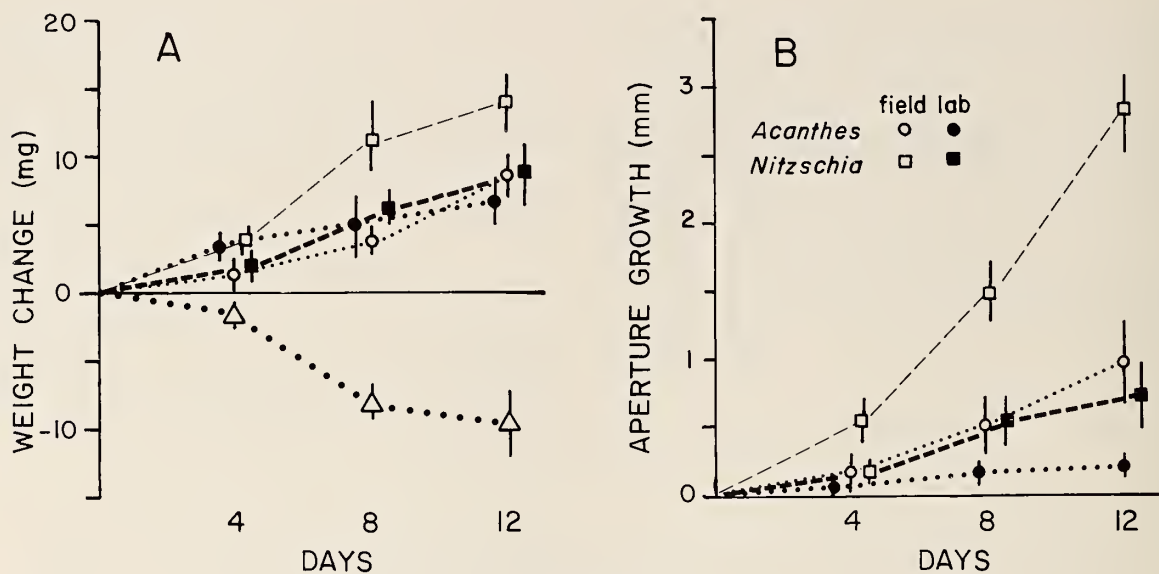


Figure 1

Growth of two groups of juvenile *Ilyanassa obsoleta* fed monocultures of the diatoms *Acanthes brevipes* and *Nitzschia* sp., or starved (triangles) (key to other symbols in insert). The snails were collected fresh from the field or maintained in the laboratory. A. Weight change. B. Growth along the aperture. Symbols show means; bars are  $\pm 1$  SD.

however. Consequently, additional experiments compared the diet of this neogastropod, which uses a crystalline style to digest plant material, to a mesogastropod, the superorder of typically herbivorous gastropods. Growth of juveniles of *I. obsoleta* was compared to that of juvenile *Littorina littorea* (Linnaeus), a herbivorous mesogastropod (LUBCHENCO, 1978; HUNTER & RUSSELL-HUNTER, 1983; WATSON & NORTON, 1985).

#### MATERIALS AND METHODS

Juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* occur together in sandy marsh habitats in Barnstable Harbor, Massachusetts. All snails used in this study were collected from a marsh tide pool in a sandy habitat (median grain 0.62 mm, 0.8% silt-clay) near the mouth of the bay. Each snail was individually numbered on the spire (total, 144 *I. obsoleta* and 130 *L. littorea*). To measure new shell growth, a line was inked on the outer shell surface along the original aperture edge with a nontoxic ink (Tech-Pen ink, Mark-Tex Corp., Englewood, New Jersey). The secretion of new shell material was measured from the ink line using an ocular micrometer ( $\pm 0.02$  mm). Snails were maintained without food (1) for 36–48 h prior to feeding or (2) for the duration of each study (controls). All studies were conducted at temperatures between 20 and 23°C and at salinities of 31–34‰.

Juvenile *Ilyanassa obsoleta* were fed monocultures of the diatoms *Acanthes brevipes* and *Nitzschia* sp. in the laboratory. Diatoms were grown under fluorescent light on autoclaved dishes (14 cm diameter) containing an enriched seawater medium (HINEGARDEN & TUZZI, 1981:229) and

washed with filtered seawater. Six snails (4–6 mm shell length) collected fresh from the field in August 1985, or eight snails (also 4–6 mm) maintained without meat or carrion at 8–12°C for a year in the laboratory, were placed into separate dishes. Snails were changed to fresh dishes every 2 days to minimize growth of bacteria on feces. Aperture growth and snail weight ( $\pm 0.002$  g) after blotting the aperture were measured every 4 days for 12 days for individuals on a diet of *Acanthes* and subsequently for 12 days on a *Nitzschia* diet. At the end of the experiment the new shell material was removed and the snails were reweighed. Effects of diet on weight change and aperture growth of snails were determined by analyses of covariance using log-transformed data and initial weight and days lapsed as covariates. Bartlett's test was used to test for homogeneity of variances in these and all other ANOVAs.

Growth of juvenile *Ilyanassa obsoleta* (4–6 mm) and juvenile *Littorina littorea* (5–7 mm) was studied in outdoor seawater tanks in August 1981. Snails were placed into compartments (4 × 4 × 4 cm) of plastic storage boxes perforated with numerous holes, too small for the snails to pass through but adequate for circulation, and maintained on the floor of the empty tanks with seawater constantly flowing over them. The snails were collected 36–48 h prior to the experiments and marked. Twenty control snails (each species) were maintained indoors without food. For single-species treatments, 10 snails of one species were placed into a compartment and provided (1) one living adult *I. obsoleta* with a green alga (*Pilinia lunatae*) growing on its shell, (2) 1.5 cm<sup>3</sup> of diatomaceous sand freshly collected from the marsh pool, or (3) both a shell and 1.5 cm<sup>3</sup>

Table 1

Analysis of covariance tables for aperture growth and weight gain in two groups of juvenile *Ilyanassa obsoleta* on two diatom monocultures. The covariates are initial shell length and days lapsed.

Source	df	Mean square	F ratio
Aperture growth <sup>1</sup>			
Group	1	5.808	47.288***
Diet	1	3.411	27.770***
Interaction	1	0.162	1.315
Covariate	2	2.417	19.675***
Error	66	0.123	
Weight gain <sup>2</sup>			
Group	1	1.478	25.363***
Diet	1	0.496	8.507**
Interaction	1	0.256	4.385*
Covariate	2	1.570	26.947***
Error	74	0.583	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

<sup>1</sup> Bartlett's test for homogeneity of variances,  $\chi^2 = 1.614$ ,  $df = 3$ ,  $P > 0.05$ .

<sup>2</sup> Bartlett's test,  $\chi^2 = 2.423$ ,  $df = 3$ ,  $P > 0.05$ .

of sand. Snails were not weighed in this experiment. Comparisons of aperture growth [ $\log_{10}(x + 1)$ ] after 8 days were made between species and diets by analysis of covariance, using shell length as a covariate. The quality and quantity of plant material on the sand and shells (five replicates each) were determined by extracting plant pigments overnight in darkness at 4°C with 10 mL of cold, 90% glass-distilled methanol after the methods of FENCHEL & STRAARUP (1971). Spectral absorbances before and after acidification were converted to mg pigment per shell or 1.5 cm<sup>3</sup> sand using the Parsons-Strickland equations (STRICKLAND & PARSONS, 1972).

Growth was also measured in two-species communities to determine if juveniles grazed the same food items. Fresh sand (1.5 cm<sup>3</sup>) was provided in compartments containing (a) 5 ( $n = 4$  compartments), 10 ( $n = 2$ ), or 20 ( $n = 1$ ) juveniles of one species, or (b) equal numbers (5 [ $n = 2$ ], 10 [ $n = 2$ ], or 20 [ $n = 1$  compartment]) of both species. Growth was measured along the aperture after 8 days. By two-way analyses of covariance, the per capita growth and the sum growth of each microcosm population (both log transformed) were compared between species using total snail density as a covariate.

## RESULTS

Juvenile *Ilyanassa obsoleta* gained weight and added shell material when fed diatom monocultures, but lost weight and added no shell material when starved (Figure 1). New shell material accounted for 33% ( $\pm 11\%$ ) of the weight increase. Field-fresh snails grew significantly more than laboratory reared snails but both groups grew faster on

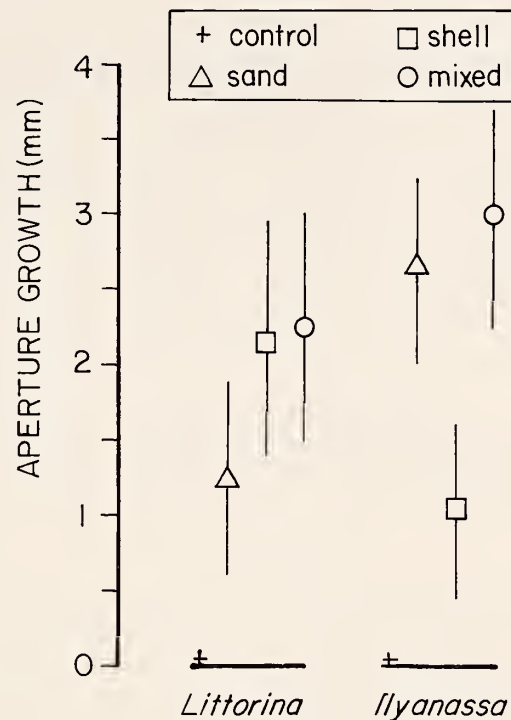


Figure 2

Aperture growth over 8 days of juvenile *Littorina littorea* and juvenile *Ilyanassa obsoleta* on diets of sand, *Pilinia* on mud snail shells, and both sand and shell; control snails were not fed. Symbols show means; bars are  $\pm 1$  SD. Key to symbols in insert.

*Nitzschia* than *Acanthes* (Table 1). A significant interaction term was due to the large weight gain of field-fresh snails on the *Nitzschia* diet.

Juveniles of *Ilyanassa obsoleta* and *Littorina littorea* grew on diets of sand microflora and *Pilinia* on mud snail shells (Figure 2). The *Pilinia* diet was richer in all plant pigments studied (Table 2). Differences in growth between species and diets were not significant (Table 3), but the significant interaction term demonstrated that the species responded differently to the diets: *L. littorea* grew slowly on sand but equally fast on *Pilinia* and the mixed diet, whereas juvenile *I. obsoleta* grew best on a mixed diet and better on sand than on *Pilinia*.

In both single and two-species systems, per capita growth of individuals on a diet of sand declined with density (Figure 3A) but total growth of microcosm populations remained constant over density (Figure 3B, Table 4). Species differences were significant: *Ilyanassa obsoleta* grew faster than *Littorina littorea*. For per capita growth, interspecific density effects were not significantly different from intraspecific effects, and the interaction term was not significant (Table 4). Thus, individuals grew at similar rates whether or not neighbors were related. Relative to monocultures, the total growth was about 50% less in mixed cultures



Table 2

Plant pigments (mg) for sand microflora (1.5 cm<sup>3</sup>) and shell epiflora (one shell); means and standard deviations of five replicates.

Pigment	Sand microflora	Shell epiflora	Shell/sand
Chlorophyll a	1.6 ± 0.2	2.8 ± 0.2	1.75
Chlorophyll b	0.19 ± 0.05	0.24 ± 0.05	1.26
Chlorophyll c	0.76 ± 0.12	1.18 ± 0.06	1.55
Carotenoids	0.70 ± 0.05	0.87 ± 0.05	1.24

(with 50% more individuals) (Figure 3B). The total population growth of *I. obsoleta* was more depressed (owing to a faster growth rate) than that of *L. littorea* in the mixed cultures.

DISCUSSION

This study found that juvenile *Ilyanassa obsoleta* added body and shell material when fed only benthic diatoms. Because benthic diatoms trigger the planktonic larvae to settle (SCHELTEMA, 1961), they are likely to be a major component of the juvenile's diet. Juveniles can detach algal and bacterial films from coarse sands (Figure 2; LOPEZ, 1980) and solid surfaces such as rocks (or glass dishes, Figure 1). However, they have difficulty manipulating fine silt particles within the buccal cavity (LOPEZ, 1980) and also do poorly on filamentous algae like *Pilinia* (Figure 2) and *Enteromorpha* (Brenchley, unpublished data) because their radula is unable to purchase flexible surfaces.

Juvenile *Ilyanassa obsoleta* are strikingly similar to juvenile *Littorina littorea* in sandy habitats of Barnstable Harbor (Brenchley, unpublished data). Both species settle into marshes during summer months and attain a similar size by autumn. The young snails graze on decaying marsh grasses and ascend marsh vegetation during high tide. Despite the propensity of *L. littorea* to graze on hard substrata,

Table 3

Analysis of covariance table for aperture growth (log transformed) of juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* on single and mixed diets of sand and shell epiflora; the covariate is initial shell length.

Source <sup>1</sup>	df	Mean square	F ratio	P
Species	1	0.0047	0.18	0.671
Diet	2	0.0650	2.53	0.089
Interaction	2	0.0842	3.28	0.046
Covariate	1	0.0016	0.06	0.803
Error	50	0.0256		

<sup>1</sup> Bartlett's test,  $\chi^2 = 5.681$ , df = 5,  $P > 0.05$ .

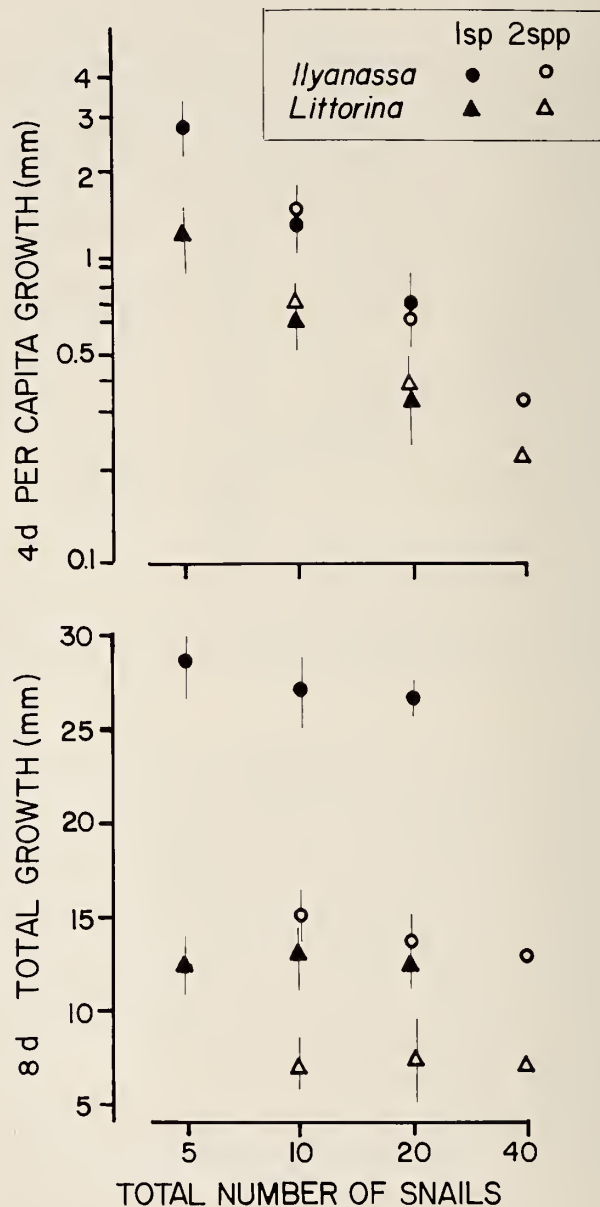


Figure 3

Aperture growth of juvenile *Littorina littorea* and juvenile *Ilyanassa obsoleta* as a function of total snail density in single and two-species systems over 8 days on a diet of diatomaceous sand. A. Per capita growth over 4-day intervals. B. Total growth of microcosm populations in 8 days. Symbols show means; bars are  $\pm 1$  SD. Key to symbols in insert.

e.g., *Pilinia* on adult mud snail shells (Figure 2), only 7% of the juveniles compared to 3% of juvenile *I. obsoleta* occur on shell substrata in the tide pool; most juveniles of both species occur on the sandy substrata.

The two taxonomic groups represented here do not nor-

Table 4

Analysis of covariance tables for aperture growth and total microcosm growth of juvenile *Ilyanassa obsoleta* and juvenile *Littorina littorea* on a diet of diatomaceous sand in single and mixed species communities. The covariate is total snail density.

Source	df	Mean square	F ratio	Comments
Per capita growth <sup>1</sup>				
Species	1	1.878	27.234***	growth <i>Ilyanassa</i> > <i>Littorina</i>
1 vs. 2 species	1	0.217	3.147	intra = interspecific effects
Interaction	1	1.415	0.021	
Covariate	1	2.608	37.821***	growth decreases with density
Error	145	0.069		
Total growth <sup>2</sup>				
Species	1	0.105	150.06***	growth <i>Ilyanassa</i> > <i>Littorina</i>
1 vs. 2 species	1	0.066	94.68***	less growth in mixed cultures
Interaction	1	0.227	32.44***	<i>Ilyanassa</i> grows less in mixed system
Covariate	1	<0.001	0.42	total growth independent of density
Error	15	0.0007		

\*\*\*  $P < 0.0001$ .

<sup>1</sup> Bartlett's test,  $\chi^2 = 6.015$ ,  $df = 3$ ,  $P > 0.05$ .

<sup>2</sup> Bartlett's test,  $\chi^2 = 5.776$ ,  $df = 3$ ,  $P > 0.05$ .

mally compete for food, owing to a divergence in diet that began during the Mesozoic. BROWN (1969) and CURTIS (1980) have speculated that the ancestral stock of *Ilyanassa obsoleta* could not compete with its more specialized, carnivorous neogastropod relatives, nor with the more efficient, microherbivorous mesogastropods. Presumably, digestion of plant foods in the neogastropod stock was dependent upon an innovation, *i.e.*, style acquisition. Results of this study suggest that because of this innovation, young *I. obsoleta* exploit the same foods as the mesogastropod *Littorina littorea*. If the density effects of Figure 3 were due to interference, *e.g.*, stress due to crowding, then the total growth of microcosm populations should have declined with increased density, but such trends were not significant (Table 4). Studies of sympatric gastropods have shown that unrelated species exploit algae differently while congeners often have similar exploitation abilities (reviewed by BRANCH, 1984). The similarities in per capita growth curves in single versus mixed systems of young *I. obsoleta* and *L. littorea* (Figure 3A) imply equal exploitative ability, providing the first example for unrelated species.

The results strongly suggest that the young *Ilyanassa* retain rather than cycle their crystalline style. Because algae cannot be digested when the style is absent, dissolution of the style would greatly reduce assimilation efficiency on a plant diet. However, the similarity in growth patterns (Figure 3A) indicates that the mud snail was as efficient in assimilating plant foods as the littorinid. There is limited evidence that young *Ilyanassa* in marsh habitats may not cycle their styles (CURTIS & HURD, 1981b), in contrast to the cyclic pattern frequently reported for large (16–25 mm), sexually mature snails (*e.g.*, CURTIS & HURD, 1981a, b).

Several workers have speculated that the success of *Ilyanassa* is due to a diverse diet, yet few have suggested how the style innovation could enhance the species' abundance. In addition to possible costs associated with the formation or dissolution of the style, the style cycling is quite costly to adult snails because much ingested material passes undigested. CURTIS & HURD (1981a) relate the species' success to its unique role in the benthic community. Despite a unique niche, the species' broad diet does not eliminate the adults' reproductive need for carrion (HURD, 1985), and the style innovation places the juveniles in competition with herbivorous snails (this study). An explanation not previously suggested is that the innovation allows the snail to invade (new) habitats and thereby avoid predators.

Studies of the snail's ecology in Barnstable Harbor suggest that only as a herbivore can the young *Ilyanassa* occupy a predator refugium in sandy intertidal habitats. The mesogastropods and littorinids in particular are tolerant of desiccation and thus can obtain refuge from most predators by inhabiting the upper tidal zones. The neogastropods are less tolerant of desiccation; most nassariids of temperate sand flats remain near or below mean low water and only the adults move into the intertidal zone (*e.g.*, KUSKINS & MANGUM, 1971; TALLMARK, 1980). Adult *I. obsoleta* are more tolerant of desiccation than the young (SCHAEFER *et al.*, 1968) and immune from attack by the shell-crushing crustaceans of the lower tide zones (BRENCHLEY, 1982, unpublished data). Susceptible to desiccation and particularly to crab predators, young *I. obsoleta* obtain refuge by settling into upper intertidal pools, seeps, and creek beds. Herbivory may be a prerequisite for marsh habitation, as drift carrion is scarce; the snails emigrate to the sand flats upon reaching maturity (Brenchley, unpublished data).

Consequently, the style innovation may permit young snails to enter a predator refugium, which may partly explain the numerical success of this ubiquitous species.

#### ACKNOWLEDGMENTS

The outdoor seawater tanks were provided by the Woods Hole Oceanographic Institution. I thank Merryl Alber for assisting in the growth studies, Naomi Culp in the pigment analyses, Patrick Leahy for providing diatom cultures, and Peter Dixon for identifying *Pilinia*. Roger Griffis, Larry Curtis, and Lynn Carpenter provided helpful comments on the manuscript. The research was supported in part by a faculty grant from the University of California, Irvine.

#### LITERATURE CITED

- BRANCH, G. M. 1984. Competition between marine organisms: ecological and evolutionary implications. *Oceanogr. Mar. Biol. Ann. Rev.* 22:429-593.
- BRENCHLEY, G. A. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. *Mar. Ecol. Prog. Ser.* 9:255-262.
- BROWN, S. C. 1969. The structure and function of the digestive system of the mud snail, *Nassarius obsoletus* (Say). *Malacology* 9:477-500.
- CRISP, M. 1969. Studies on the behavior of *Nassarius obsoletus* (Say) (Mollusca, Gastropoda). *Biol. Bull.* 136:355-373.
- CURTIS, L. A. 1980. Daily cycling of the crystalline style in the omnivorous, deposit-feeding estuarine snail *Ilyanassa obsoleta*. *Mar. Biol.* 59:137-140.
- CURTIS, L. A. & L. E. HURD. 1979. On the broad nutritional requirements of the mud snail, *Ilyanassa (Nassarius) obsoleta* (Say), and its polytrophic role in the food web. *Jour. Exp. Mar. Biol. Ecol.* 4:1-9.
- CURTIS, L. A. & L. E. HURD. 1981a. Nutrient procurement strategy of a deposit-feeding estuarine neogastropod, *Ilyanassa obsoleta*. *Estuarine Coast. Shelf Sci.* 13:277-285.
- CURTIS, L. A. & L. E. HURD. 1981b. Crystalline style cycling in *Ilyanassa obsoleta* (Say) (Mollusca: Neogastropoda): further studies. *Veliger* 24:91-96.
- DIMON, A. C. 1905. The mud snail: *Nassa obsoleta*. Cold Spring Harbor Monogr. 5:1-50.
- FENCHEL, T. & B. J. STRAARUP. 1971. Vertical distribution of photosynthetic pigments and the penetration of light in marine sediments. *Oikos* 22:172-182.
- HINEGARDEN, R. T. & M. M. R. TUZZI. 1981. Laboratory culture of the sea urchin *Lytechinus pictus*. Pp. 291-302. *In*: National Research Council, Marine Invertebrates. National Academy Press: Washington, D.C.
- HUNTER, R. D. & W. D. RUSSELL-HUNTER. 1983. Bioenergetic and community changes in intertidal Aufwuchs grazed by *Littorina littorea*. *Ecology* 64:761-769.
- HURD, L. E. 1985. On the importance of carrion to reproduction in an omnivorous estuarine neogastropod, *Ilyanassa obsoleta* (Say). *Oecologia* 65:513-515.
- JENNER, C. E. 1956. The occurrence of a crystalline style in the marine snail, *Nassarius obsoletus*. *Biol. Bull.* 111:304.
- KUSKINS, L. J. & C. P. MANGUM. 1971. Responses to low oxygen conditions in two species of the mud snail *Nassarius*. *Comp. Biochem. Physiol.* 39A:421-435.
- LUBCHENCO, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preferences and algal competitive ability. *Amer. Natur.* 112:23-39.
- LOPEZ, G. R. 1980. The availability of microorganisms attached to sediment as food for some marine deposit-feeding molluscs, with notes on microbial detachment due to the crystalline style. Pp. 387-405. *In*: K. R. Tenore & B. C. Coull (eds.), Marine benthic dynamics. Univ. South Carolina Press: Columbia.
- Noguchi, H. 1921. *Cristispira* in North American shellfish. A note on a spirillum found in oysters. *Jour. Exp. Med.* 34:295-315.
- ROBERTSON, J. R. 1979. Evidence for tidally correlated feeding rhythm in the eastern mud snail, *Ilyanassa obsoleta*. *Nautilus* 93:38-40.
- SCHAEFER, C. W., N. L. LEVIN & P. MILCH. 1968. Death from desiccation in the mud-snail, *Nassarius obsoletus*: effects of size. *Nautilus* 82:28-31.
- SHELTEMA, R. S. 1961. Metamorphosis of the veliger larvae of *Nassarius obsoletus* (Gastropoda) in response to bottom sediment. *Biol. Bull.* 120:92-108.
- SHELTEMA, R. S. 1964. Feeding habits and growth in the mud snail *Nassarius obsoletus*. *Chesapeake Sci.* 5:161-166.
- STRICKLAND, J. D. H. & T. R. PARSONS. 1972. A practical handbook of seawater analysis. Fish. Res. Bd. Canada, Bull. 167.
- TALLMARK, B. 1980. Population dynamics of *Nassarius reticulatus* (Gastropoda, Prosobranchia) in Gullmar Fjord, Sweden. *Mar. Ecol. Prog. Ser.* 3:51-62.
- WATSON, D. C. & T. A. NORTON. 1985. Dietary preferences of the common periwinkle, *Littorina littorea*. *Jour. Exp. Mar. Biol. Ecol.* 88:193-211.
- YONGE, C. M. 1930. The crystalline style of the Mollusca and a carnivorous habitat cannot normally co-exist. *Nature* 125:444-445.